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Body awareness, voluntary physiological regulation, and their modulation by contemplative mental training

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Abstract

In this dissertation, I investigate interactions between mental and bodily processes, specifically by studying the influence of contemplative mental training (CMT) on interoception (inner body sensing) and physiological regulation. In a large-scale mental training study (n = 332, training durations 3–9 months), the *ReSource Project*, I find that CMT increases interoceptive accuracy in the training cohorts, but not in a retest control cohort. These increases in interoceptive accuracy co-occur with and predict improvements in emotional awareness. In line with these objective data on interoception, participants self-report training-related benefits on multiple dimensions of body awareness. The strongest changes occur in the ability to sustain attention to body sensations and the use of this ability to identify and regulate emotions. I also introduce a novel biofeedback task that measures the ability to voluntarily upregulate high frequency heart rate variability (HF-HRV), indicative of voluntary parasympathetic control. Cross-sectional data of the *ReSource Project* show that individual differences in voluntary parasympathetic control are related to the oxytocin receptor gene rs53576 polymorphism and correlate to individual differences in altruistically motivated behavior. Furthermore, CMT improves various aspects of voluntary HF-HRV regulation, with modulation of these improvements by rs53576 genotype. An additional investigation in cross-sectional data shows that subjective retrospective reports of an emotionally arousing experience partially mirror the objectively measured bodily arousal during the actual experience. Individual differences in this mind–body coherence are related to individual differences in interoceptive accuracy. Together, these studies highlight the tight interplay between physiological and mental processes and show how CMT improves inner body sensing and voluntary physiological regulation.

Keywords: interoception, physiological regulation, vagus, heart rate variability, meditation, mindfulness, biofeedback, genes, prosocial behavior, virtual reality

Deutsche Zusammenfassung

In dieser Dissertation untersuche ich das Zusammenspiel mentaler und körperlicher Prozesse, insbesondere den Einfluss von kontemplativem Mentaltraining (KMT) auf Interozeption (innerliches Spüren des Körpers) und physiologische Regulation. In einer großangelegten Trainingsstudie (n = 332, Trainingsdauer 3-9 Monate), der *ReSource-Studie,* zeige ich, dass KMT die interozeptive Genauigkeit in den Trainingskohorten erhöht, nicht jedoch in einer Retest-Kontrollgruppe. Die Steigerungen in interozeptiver Genauigkeit gehen mit Veränderungen im emotionalen Gewahrsein einher und sagen diese voraus. Im Einklang mit diesen Befunden berichten die Studienteilnehmenden von positiven Veränderungen in verschiedenen Dimensionen des Körpergewahrseins. Diese betreffen vor allem die Fähigkeit, Aufmerksamkeit auf Körperempfindungen aufrechtzuerhalten sowie deren Gebrauch zur Emotionserkennung und -regulation. Ich beschreibe eine neuentwickelte Biofeedback-Aufgabe, welche die Fähigkeit misst, willentlich die hochfrequente Herzratenvariabilität (HF-HRV) hochzuregulieren, wodurch die willentliche parasympathische Kontrollfähigkeit (WPK) indiziert wird. Ich zeige, dass individuelle Unterschiede in WPK mit dem Oxytocin-Rezeptorgen-Polymorphismus rs53576 zusammenhängen und mit individuellen Unterschieden im altruistisch motivierten Verhalten korrelieren. WPK wird durch KMT verbessert, wobei diese Verbesserungen durch den rs53576 Genotyp moduliert werden. In einer weiteren Untersuchung zeige ich, dass retrospektive, subjektive Berichte über eine emotional erregende Erfahrung teilweise die objektiv gemessene körperliche Erregung widerspiegeln. Das Ausmaß dieser körperlich-mentalen Kohärenz ist abhängig von der interozeptiven Genauigkeit. Zusammengenommen vertiefen diese Studien unser Verständnis des Zusammenspiels von physiologischen und mentalen Prozessen und zeigen wie KMT das innerliche Spüren des Körpers und die willentliche physiologische Regulation verbessert.

Schlüsselwörter: Interozeption, physiologische Regulation, Vagus, Herzratenvariabilität,

Meditation, Achtsamkeit, Biofeedback, prosoziales Verhalten, virtuelle Realität

Eingereichte Einzelarbeiten

Bornemann, B., & Singer, T. (2016). Taking time to feel our body: Steady increases in heartbeat perception accuracy and decreases in alexithymia over 9 months of contemplative mental training. *Psychophysiology*. [Study 1] – doi: 10.1111/psyp.12790

Bornemann, B., Herbert, B. M., Mehling, W. E., & Singer, T. (2015). Differential changes in self-reported aspects of interoceptive awareness through 3 months of contemplative training. *Frontiers in Psychology*, *5*, 1504. [Study 2] – doi: 10.3389/fpsyg.2014.01504

McCall, C., Hildebrandt, L. K., **Bornemann, B.**, & Singer, T. (2015). Physiophenomenology in retrospect: Memory reliably reflects physiological arousal during a prior threatening experience. *Consciousness and Cognition*, *38*, 60-70. [Study 3] – doi: 10.1016/j.concog.2015.09.011

Bornemann, B., Kok, B. E., Böckler, A., & Singer, T. (2016). Helping from the heart: Voluntary upregulation of heart rate variability predicts altruistic behavior. *Biological Psychology*, *119*, 54-63. [Study 4] – doi: 10.1016/j.biopsycho.2016.07.004

Bornemann, B., Kok, B.E., Kovacs, P., & Singer, T. (in preparation). Voluntary upregulation of heart rate variability through biofeedback is improved by mental training and modulated by oxytocin receptor gene rs53576 polymorphism. [Study 5] – manuscript available from author

Content

"If the body is not mastered [by meditation], the mind cannot be mastered.

If the body is mastered, mind is mastered."

– Majjhima Nikaya, sutta 36

Introduction

What is the relationship between mental and bodily phenomena? Does familiarity with our own body help us in understanding our thoughts, emotions, and other mental processes? Conversely, does understanding of our mental processes have an impact on our body or our ability to regulate bodily processes?

These kinds of questions motivate the investigations of this dissertation. They are at the core of the burgeoning field of psychosomatic medicine that has recognized the tight coupling of mental and bodily processes and its importance for the explanation and treatment of both physical and psychological disease (Astin, 2004; Kuyken et al., 2015; Mehling et al., 2011; Röhricht, Gallagher, Geuter, & Hutto, 2014; Wahbeh, Elsas, & Oken, 2008; Wolsko, Eisenberg, Davis, & Phillips, 2004). They are also linked to philosophical questions about the body and its relation to conscious experience (McLaughlin, Beckermann, & Walter, 2009) or the feeling of "selfhood" (Metzinger, 2007). These questions have been asked since ancient times in the West (Aristotle, ~300BC/1961; Plato, ~400BC/1925), and the East ("Majjhima Nikaya," ~600BC/2014; Nagarjuna, ~200CE/2002) and continued to fascinate scholars through the ages (Descartes, 1641/2009; Spinoza, 1677/2006) up to the present day (Dennett, 1993; Kim, 2000).

In this dissertation, I will take an empirical approach to distinct aspects of these questions by studying whether and how the perception of our body is affected through mental contemplative training. This will be done by using both objective and subjective markers of body awareness. I will also investigate the relationship of these changes to changes in emotional awareness. Furthermore, I will study the alignment of physiological signals and subjective reports during emotional experience as well as the dependency of this alignment on body perception. Finally, I will introduce a novel measure to quantify the ability of voluntarily modifying physiological activity and investigate both the genetic basis of this regulatory ability and its relation to social behavior. I will then study the malleability of voluntary physiological regulation through contemplative mental training.

In the following sections of this introduction (Section 1), I will provide the general background of these investigations and define key terms. In Section 2, I will summarize the empirical investigations. In Section 3, I will discuss these findings in context, including their societal and philosophical implications.

Interoception

Interoception has been defined as the "sense of the physiological condition of the body" (Craig, 2002; also see Sherrington, 1910, p.320ff., for an early definition). This may involve conscious perception of muscle tension and visceral processes, but also subconscious transmission of signals about blood sugar concentration or body temperature (Tsakiris & Critchley, 2016). A broader definition, which I will endorse in this dissertation, describes interoception as "the process of receiving, accessing and appraising internal bodily signals" (Farb et al., 2015). Just like the process of vision is typically understood to go beyond the mere reception of light signals (Findlay & Gilchrist, 2003), the process of interoception according to this definition includes more than the mere reception of signals from the body. Research in the last century has generated a wealth of knowledge about the process of vision, including various analysis steps of the incoming signals by cortical areas that react to specific colors, forms, or movements (Livingstone & Hubel, 1987), as well as interactions of the "bottom-up" signal processing by "top-down" processes such as attention or memory (Bar, 2003; Desimone & Duncan, 1995). Although our knowledge about the process of interoception is not as refined yet, the last decades have seen an upsurge of interest in the topic, with a sixfold increase in publications on interoception in the last 10 years (Tsakiris & Critchley, 2016).

As a result of this research, a neurophysiological understanding of the processes of interoception is emerging. This process includes various peripheral receptor cells (e.g., baro- and chemoreceptors and C-fiber endings), the transmission of their signals along the spinal cord (particularly lamina 1), and the network of subcortical and cortical structures that process these signals, including, most importantly, ventromedial thalamic nuclei, the parabrachial nucleus, the nucleus of the solitary tract, the insula, and anterior cingulate cortices (Critchley & Harrison, 2013; Strigo & Craig, 2016). Similar to the modulatory effects discovered for vision, we are beginning to understand how this bottom-up stream of bodily information is in constant interaction with higher-order processes (Ainley, Apps, Fotopoulou, & Tsakiris, 2016; Blanke, 2012; Lopez, Halje, & Blanke, 2008; Michalak, Rohde, & Troje, 2015). These interactions are particularly central to models of interoceptive inference that have been proposed and elaborated by various researchers in the last few years (Barrett & Simmons, 2015; Seth, 2013; Seth & Friston, 2016). Models of interoceptive inference assume that the brain constantly produces "expectations" (Bayesian priors) about the physiological state that determine how signals from the body are processed. These models thus offer the framework for the broader understanding of interoception as a perceptual process in which bottom-up information is in constant interaction with top-down processes, such as attention, cognition, and emotion.

Definitions

Despite the recent advances in the field, no full consensus has been achieved regarding the terminology used to describe the various aspects of interoception. There are several recently published and widely cited articles (Farb et al., 2015; Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015; Mehling, 2016) in which the authors have suggested definitions to which I will orient in my usage of terms in this dissertation. All of the cited authors define <u>interoceptive accuracy</u> (IAcc) as the ability to accurately perceive interoceptive signals as measured by objective tests. Examples are the accurate and objectively determined ability to perceive one's own heartbeat signals (Brener & Jones, 1974), gastric movements (Herbert, Muth, Pollatos, & Herbert, 2012), or breathing sensations (Daubenmier, Sze, Kerr, Kemeny, & Mehling, 2013).

Self-reported interoception, as assessed through questionnaires and interviews, has received different labels by the various authors. Garfinkel et al. call this aspect *interoceptive sensibility*. This term has, however, been criticized by Mehling (2016) for various reasons, including the ambiguity of the word "sensibility" as it has been used in philosophical, scientific, and literary discourses and its general usage in everyday language. Instead, I will use the term interoceptive awareness (IAw), which I understand to have multiple dimensions (Mehling et al., 2009; Mehling et al., 2012) according to the broader definition of interoception endorsed above, including different styles of attending to and appraising bodily signals (Farb et al., 2015).

Finally, Farb et al. speak of *coherence* to denote the degree to which subjectively reported data and objective physiological data align. An example is the intraindividual correlation of subjectively reported feelings with the objectively recorded physiological arousal in the same time frame (Golland, Keissar, & Levit-Binnun, 2014; Mauss, Levenson, McCarter, Wilhelm, & Gross, 2005; Sze, Gyurak, Yuan, & Levenson, 2010). To clearly signify which type of coherence is meant here, I will call it psychophysiological coherence.

The body and emotion

More than 100 years ago, William James postulated that emotional feelings can be equated to the perception of physiological changes (James, 1884; also see Lange, 1885). Since then, there has been an ongoing debate in psychology regarding the relationship of bodily perceptions and emotions (Cannon-Bard theory of emotions, Cannon, 1927; Schachter-and-Singer theory of emotions, Schachter & Singer, 1962; stress appraisal models, Lazarus & Folkman, 1984; the Somatic Marker Hypothesis, Damasio, Everitt, and Bishop, 1996; predictive coding models of interoceptive inference, Ainley et al., 2016; Barrett & Simmons, 2015; Seth, 2013). By now, a host of research has demonstrated a link between bodily and emotional awareness (Craig, 2009; Wiens, 2005). In particular, higher IAcc has been linked to more intense emotional experience (Pollatos, Herbert, Matthias, & Schandry, 2007; Pollatos, Traut-Mattausch, Schroeder, & Schandry, 2007; Schandry, 1981), a stronger focus on the arousal component of these experiences (Barrett, Quigley, Bliss-Moreau, & Aronson, 2004), better identification of one's own emotions (Herbert, Herbert, & Pollatos, 2011), and stronger influence of bodily signals on decision-making (Dunn et al., 2010). Neuroscience has substantiated these findings by demonstrating an overlap between the processing of body signals and emotions in the human brain, particularly the anterior insula (Bird et al., 2010; Craig, 2004; Silani et al., 2008; Singer, Critchley, & Preuschoff, 2009; Terasawa, Fukushima, & Umeda, 2013; Zaki, Davis, & Ochsner, 2012). Additionally, the anterior cingulate cortex has been implicated in both interoception and emotion (Craig, 2002; Critchley & Harrison, 2013; Pollatos, Gramann, & Schandry, 2007; Wiens, 2005). The anterior cingulate cortex is also strongly involved in the regulation of the autonomic nervous system (Benarroch, 2012; Critchley, Tang, Glaser, Butterworth, & Dolan, 2005; Gianaros et al., 2005; Matthews, Paulus, Simmons, Nelesen, & Dimsdale, 2004), another aspect of mind–body interactions in emotion, of which the following section reviews aspects that are relevant for the research of this dissertation.

Physiological regulation: heart rate variability

All organs, muscles, and blood vessels are in constant interaction with the brain via the autonomic nervous system (ANS). The ANS is subdivided into a sympathetic and a parasympathetic branch. A heuristic description is that sympathetic activation prepares the organism for energy intensive activities including cognitive and physical efforts. Parasympathetic activity prepares the organism for rest, restorative functions, and quiet activities (for details on ANS function see Robertson, Biaggioni, Burnstock, Low, and Paton, 2012, and for details on ANS–brain interactions see Benarroch, 1993; Hagemann, Waldstein, and Thayer, 2003; Robertson et al., 2012; Strigo and Craig, 2016).

On the peripheral level, activity of the ANS can be measured non-invasively through heart rate variability (Akselrod et al., 1981; Pomeranz et al., 1985; Task-Force, 1996). The heart constantly receives inputs from both the sympathetic and the parasympathetic branch of the ANS, causing it to beat faster or slower (Levy, 1971). Sympathetic input to the cardiac pacemaker cells is noradrenergic and results in acceleration, with effective transmission typically taking at least 1 second (Jose & Taylor, 1969). Parasympathetic (specifically vagal) inputs to the heart, however, are transmitted within milliseconds using the neurotransmitter acetylcholine (Dellinger, Taylor, & Porges, 1987). Thus, rapid interactions between the brain and body usually rely on parasympathetic activity.

Heart rate variability (HRV), particularly in its parasympathetic aspects, quantified as high frequency heart rate variability (HF-HRV), marks the ability of an organism to flexibly adjust physiological processes in the face of changing demands. According to the model of Neurovisceral Integration (Thayer & Lane, 2009), adjustments in HF-HRV covary with activity in the (medial) prefrontal cortex and the amygdala (Thayer, Ahs, Fredrikson, Sollers, & Wager, 2012), and are indicative of regulatory processes in attention and emotion. This hypothesis is backed up by a wealth of research demonstrating links of HF-HRV to attention (Duschek, Muckenthaler, Werner, & del Paso, 2009; Mathewson et al., 2010), self-control (Segerstrom & Nes, 2007), and emotion-regulation (Appelhans & Luecken, 2006; Butler, Wilhelm, & Gross, 2006). Low HRV is also characteristic of many psychopathologies, such as depression (Kemp et al., 2010), anxiety (Friedman, 2007), and posttraumatic stress disorder (PTSD; Minassian et al., 2014). HRV has also been described as an integrated marker of physical health (Thayer et al., 2012). Indeed, the literature on this is vast with several prospective studies demonstrating that low HRV is a powerful predictor of all-cause mortality (Dekker et al., 1997; May & Arildsen, 2011).

The Polyvagal Theory (Porges, 2003a, 2003b, 2007) additionally highlights the role of the vagus (the largest parasympathetic nerve) for social behavior. According to this theory, vagal activity is implicated in “immobilization without fear” (Porges, 2003b), that is a calm, attentive mode of social interaction closely related to “positive social engagement” (Porges, 2003b). These types of interaction seem particularly important for care-giving behaviors, be they towards offspring or towards non-related living beings. This is underlined by the innervation of the vagus through the neuropeptide oxytocin (Boccia, Petrusz, Suzuki, Marson, & Pedersen, 2013; Carter, 2014; Tribollet, Charpak, Schmidt, Dubois-Dauphin, & Dreifuss, 1989), a hallmark of the mammalian “care-giving system” (Depue & Morrone-Strupinsky, 2005; Panksepp, 2006). It is further corroborated by the observation that increases in HF-HRV accompany human care-giving and altruistic behavior in humans (Barraza, Alexander, Beavin, Terris, & Zak, 2015; Gill & Calkins, 2003; J. G. Miller, Kahle, & Hastings, 2015; Stellar, Cohen, Oveis, & Keltner, 2015).

Contemplative mental training

The term contemplative mental training (CMT) describes a group of practices that aim at understanding conscious experience by first-person investigation (~introspection) and the deliberate cultivation of mental qualities, such as concentration, mental clarity, equanimity, or compassion. The most widely studied forms are mindfulness practices, particularly as taught in courses of Mindfulness Based Stress Reduction (MBSR, Kabat-Zinn, 1990) or variants thereof. A common definition of mindfulness is “paying attention in a particular way: on purpose, in the present moment, and non-judgmentally” (Kabat-Zinn, 1994, p.4). Thousands of studies have demonstrated positive effects of mindfulness-based training, ranging from measures of attention, cognition, and emotion (for a meta-analysis see Sedlmeier et al., 2012), to measures of brain structure and function (for meta-analyses see Fox et al., 2016; Fox et al., 2014), other biological markers (for a meta-analysis see Schutte and Malouff, 2014), and beneficial effects in the treatment of various mental and physical disorders (for meta-analyses see Bohlmeijer, Prenger, Taal, and Cuijpers, 2010, and Khoury et al., 2013).

This broad range of effects suggests that mindfulness operates on several different levels. These are already reflected in the definition, which points to several components of mindfulness (also see Shapiro, Carlson, Astin, and Freedman, 2006): There is at least an attentional component (“paying attention”) and an affective or reactive component (“non-judgementally”). Furthermore, “on purpose” suggests a certain cognitive orientation, which may entail an investigative or insight-oriented mindset (Bishop et al., 2004). As I will describe below, the *ReSource Project* aimed at taking these components apart by delivering three training modules which tackle, broadly speaking, attentional and interoceptive aspects, affective aspects, and cognitive or insight-oriented aspects. The fundamental role of body awareness in all three types of practice will be discussed below.

Main research questions

The central question of this dissertation is whether and how mind–body interactions are affected by CMT. Does intensive contemplation of mind–body events lead to greater accuracy in their detection (IAcc)? Are such changes related to changes in emotional awareness? How does CMT influence modulatory top-down processes, such as attention allocation to bodily signals and their appraisal (multiple aspects of IAw)? Does contemplative training enhance the ability to induce physiological changes at will? We were particularly interested in the induction of parasympathetic (vagal) states, because the calm and prosocial emotional-motivational state that is associated with increased vagal activity was an expected outcome of the training (see Study 5) and could have important implications for individual health and social coherence. We thus aimed at developing a task that would allow us to measure voluntary parasympathetic regulation. One goal was to gauge the validity of this task through behavioral and biological markers. Subsequently, we investigated changes in regulatory performance through CMT. As a cross-sectional contribution to the field, we used the large data set of the *ReSource study* to investigate the question of whether psychophysiological coherence is related to IAcc.

Empirical Studies

In this section, I will summarize the specific backgrounds, methods, and results of the five empirical investigations subsumed in this dissertation. Before that, I will give a brief summary of the *ReSource Project,* in the context of which the studies were conducted.

The *ReSource Project*

The *ReSource Project* (Singer et al., 2016) is a large-scale longitudinal study on CMT, which was conducted in Berlin and Leipzig by the department of Social Neuroscience of the Max Planck Institute of Human Cognitive and Brain Sciences, Leipzig, under the direction of Prof. Dr. Tania Singer. It is the largest longitudinal study on CMT completed worldwide, with over 300 participants and training durations of up to 9 months. There are three different modules in the training: Presence, Affect, and Perspective. Compared to earlier investigations, the design of the study has three major advantages: First, by separating different types of contemplative practice in the three modules and comparing their effects, more specific investigations about the efficacy of certain practice elements can be made, as compared to earlier studies, in which these elements were often conflated. Second, the temporal intensity (9 months as compared to 2 months in many earlier studies) and large sample size allow for demonstration of subtle cumulative effects that would go undetected after shorter training or with a smaller sample. Third, the multitude of measures (see Singer et al., 2016, chapter 8) allows the characterization of training-induced changes on different levels of description, such as subjective feeling, behavior, and physiological processes, as well as their interactions. The following sections briefly describe the content of the training and the study design.

Training contents of the ReSource Project

There are three different modules in the *ReSource* training: Presence, Affect, and Perspective. In all of these training modules, body sensations allow practitioners to ground awareness in the present moment and to remain in contact with their internal reality. Thus, all of the modules could have effects on interoception and physiological regulation. This bodily focus is particularly explicit in the Presence module. The two core processes of this module are *attention* and *interoceptive awareness*. The core exercises are Breathing Meditation (Wallace, 2006) and Body Scan (Hart, 1987; Kabat-Zinn, 1990). In the Breathing Meditation, participants focus on the sensations of their breathing, typically in a specific body region such as the nostrils or abdomen. Whenever attention has strayed, participants gently direct their attention back towards the breathing sensations. In the Body Scan, participants connect with sensations from throughout their body by successively guiding their attention through different body parts. Participants typically lie on their backs with their eyes closed and simply notice body sensations from the bottom of the feet to the top of the head. The instructions are not to label or think about body sensations, but simply to pay attention to their sensorial qualities (that is, to interocept). In the Affect module, participants cultivate an attitude of *compassion, care and gratitude*, as well as *prosocial motivation*, and learn *acceptance of difficult emotions* (Brach, 2003). The two core practices in this module are Loving-kindness Meditation (Salzberg, 1995) and a contemplative partner exercise called the Affect Dyad. In Loving-kindness Meditation, the practitioner cultivates an attitude of benevolence and care for oneself and others. The practice typically begins by bringing to mind a being (such as a person or an animal), to which the practitioner naturally experiences feelings of love and care. This attitude is then extended towards oneself, close others, people who are of no clear valence to the participant, or experienced as challenging. Throughout the practice, the participant is advised to retain a gentle and open inner stance toward all upcoming experiences, particularly when difficult emotions such as anger, resentment, or self-criticism arise, as is common in this type of practice (Gilbert, 2010; Salzberg, 1995). The Affect Dyad is a partner exercise, which could be described as a loud meditation: Two people sit in front of each other and take turns in contemplating the feelings they experienced during a difficult situation and during a gratitude-eliciting situation of the last 24 hours. While the speaker describes the situation, their feelings, and body sensations to their partner, the listener simply keeps eye contact and listens mindfully. Throughout both exercises body sensations are used to stay connected to the present-moment affective experience. In the Perspective module, the core processes targeted by the training are *metacognition*, *perspective-taking of the self*, and *perspective-taking of others*. The two core exercises are an Observing-thoughts Meditation and a partner exercise called the Perspective Dyad. In the Observing-thoughts Meditation (Fronsdal, 2001, pp.57ff; Kabat-Zinn, 1990; Krishnamurti, 1993), participants observe their thoughts as mental events. In the initial phases of this practice, participants mentally label or classify thoughts according their content using dimensions such as past/future, self/other, positive/negative. In later phases of the practice, the focus is on the observation of the thought process as a naturally occurring event, similar to the coming and going of a sound or a body sensation. The Perspective Dyad is a contemplative partner exercise in which partners take turns to describe a situation that occurred within the last 24 hours while taking the perspective of a randomly allotted, but previously self-ascribed, inner part (~personality aspect; see Holmes, 2007). The partner listens mindfully and tries to identify the inner part from which the situation is described. Thus, while the speaker learns how to take perspective of themselves, the listener trains taking the perspective of the other, or Theory of Mind (Frith & Frith, 2005). The framework of inner parts is taken from the Internal Family System (Holmes, 2007; Schwartz, 1997), a concept from systemic therapy, which parallels concepts of other widely used therapeutic approaches, such as Schema Therapy (Young, Klosko, & Marjorie, 2003) and Transactional Analysis (Novey, 1999). Throughout both exercises, participants may use attention to breathing and body sensations to focus more clearly on the present moment and to perceive their thinking processes as a presently-occurring event within the larger context of their experience, rather than reifying them (taking their contents for reality; Dahl, Lutz, and Davidson, 2015). Participants thus approximate states of cognitive de-fusion (Luoma & Hayes, 2002) or decentered thinking (Fresco et al., 2007), which is an important training goal in the Perspective module. For the importance of body sensations in this transformation of the practitioner's relationship to thoughts and mental constructs also see Kerr, Sacchet, Lazar, Moore, and Jones (2013); Fronsdal (2001), pp.51ff. For a more in-depth description of the rationale behind each module see Singer et al. (2016), chapters 2 and 3.

Design, timeline, and training setting in the ReSource Project

Each of the three modules comprises a 3-day silent residential retreat, 13 weekly 2-hour sessions, and daily practice of about 30 minutes. The weekly sessions were facilitated by 17 experienced meditation teachers and psychotherapists, who always taught in teams of two (Singer et al., 2016, chapter 5). Participants were taught in groups of about 20 participants in both Leipzig and Berlin. For the home practice, both single meditations and dyadic exercises were facilitated by a web-based platform and a smartphone app.

Training cohort 1 (TC1; n = 80) underwent the modules in the order of Presence, Affect, Perspective. Training cohort 2 (TC2; n = 81) underwent the modules in the order of Presence, Perspective, Affect (total training duration for TC1 and TC2: 9 months). Training cohort 3 (TC3; n = 81) only underwent the Affect module (duration: 3 months). Two retest control cohorts (pooled in all analyses, RCC; n = 91) did not undergo any training but completed all measurements in comparable temporal distance to the training cohorts. Participants were screened and interviewed to be mentally and physically healthy. All cohorts were matched with regard to mean age, sex, socio-economic status, and various personality traits. The design is described in more detail in Singer et al. (2016), chapter 4. Recruitment and selection procedure are detailed in Singer et al. (2016), chapter 7.

Measurements always took place in weeks 7–13 of each module. Specifically, all the data from physiological recordings reported in this dissertation were taken in week 13. Questionnaires could be filled out between weeks 7 and 13, and the behavioral data referred to in this dissertation were assembled between weeks 7 and 12.

All of the studies described below utilized either the full T0 dataset or the full diachronic sample (T0 to T3) of the *ReSource Project*, with the exception of Study 2, where additional participants were recruited to increase the sample size for the validation of the novel measure that was used in the study.

Study 1: Changes in interoceptive accuracy through contemplative mental training and its relationship to changes in emotional awareness

In this study, we investigated whether IAcc is malleable through mental contemplative practice. We measured the ability to perceive one's own heartbeat, which is the most widely used approach to assess IAcc. Specifically, we used the mental tracking procedure (Schandry, 1981). In this procedure, participants are asked to count the number of heartbeats in intervals of varying duration while an electrocardiogram (ECG) is acquired, allowing quantification of heartbeat perception accuracy (HBPa). Previous studies which used this and similar measures of HBPa had not found any effects of mental contemplative training (Khalsa et al., 2008; Melloni et al., 2013; Nielsen & Kaszniak, 2006; Parkin et al., 2013). However, these studies had used small samples and short interventions, or cross-sectional designs with long-term meditation practitioners with unclear extents of bodily focus in their daily practice. Thus, a longitudinal study in a large sample undergoing a long period of CMT utilizing attention to body sensations was necessary to investigate the hypothesis that this type of training fosters HBPa.

We were also interested in whether the training increases emotional awareness, and if so, whether these changes are related to changes in HBPa. To assess emotional awareness, we used the Toronto Alexithymia Scale (TAS; Bagby, Parker, & Taylor, 1994), which measures alexithymia (Nemiah, Freyberger, & Sifneos, 1976), a trait characterized by difficulties in identifying and describing feelings, as well as an externally oriented thinking style. Two earlier studies have reported reductions in TAS through contemplative training, specifically 8 weeks of MBSR, and observed relationships of TAS reductions with increases in insula volume (Arias, Justo, & Granados, 2010; Santarnecchi et al., 2015). However, a relationship between training-induced increases in IAcc and decreases in alexithymia had never been reported.

We found that HBPa increased in the training cohorts but not in the retest control cohort, with the interaction reaching statistical significance after 6 months of training and continuing to increase until the end of the training where a total effect size of Cohen's d = .273 was reached. The three modules did not differ significantly in their effectiveness in increasing HBPa. TAS scores of the trained participants decreased over the training (total effect size d = -.331). Post-hoc analysis revealed that TAS was only decreased through the Presence and the Affect module, not through the Perspective module. Interestingly, changes in HBPa predicted concomitant and subsequent decrements in the TAS. Concomitant changes were only observed in the initial training phase (T0 to T1) and specifically during the Presence module, not during the Affect module.

Subgroup analyses revealed that participants with initially lower HBPa showed stronger increases. Baseline dependency of change was even more pronounced for alexithymia, where participants with initially higher TAS values showed much stronger decrements through the training (up to 1 standard deviation for participants whose TAS scores were close to clinical significance). TAS scores of >60 at screening had been an explicit exclusion criterion for our sample. The effect size of training-induced TAS decrements is thus probably a conservative estimate of these effects in the general population.

To summarize, our study indicates that CMT may enhance IAcc (measured as HBPa) and emotional awareness (measured by the TAS) and that those two effects are interrelated.

Study 2: Changes in multiple aspects of interoceptive awareness through 3 months of Presence training

In this study, we investigated changes in multiple aspects of IAw through contemplative practice. We focused on the Presence module, which is the one that most directly targets interoceptive capacities.

Most available questionnaires capture only one aspect of IAw (L. C. Miller, Murphy, & Buss, 1981; Shields, Mallory, & Simon, 1989), do not clearly differentiate between functional and dysfunctional aspects of IAw (Porges, 1993), or conflate different aspects of IAw in one scale (see Mehling et al., 2009, for a review). A previous study using several of these instruments (Sze et al., 2010) found higher IAw in experienced meditators. However, the exact nature of these differences seems insufficiently characterized by the employed scales. The results of three prospective, qualitative studies on the effects of CMT using content-analyses of journal entries and open questions (Landsman-Dijkstra, van Wijck, Groothoff, & Rispens, 2004; Morone, Lynch, Greco, Tindle, & Weiner, 2008; Schure, Christopher, & Christopher, 2008) suggest that participants experience a wide range of benefits, such as improved attention, higher awareness of emotions and of the mind–body connection, and a higher propensity to "listen to their bodies". However, the relative size of the reported benefits cannot be quantified by these data. To overcome the problems of earlier questionnaires described above, Mehling et al. constructed the Multidimensional Assessment of Interoceptive Awareness (MAIA) based on analyses of the existing questionnaires, discussions in focus groups of advanced and lay mind–body practitioners, and iterative psychometric testing (Mehling et al., 2012; Mehling et al., 2011). Because the questionnaire did not exist in German, we translated it then investigated its reliability and validity in a large and diverse sample (total n = 1076).

We found the German version of the MAIA scales to display internal consistencies similar to those of the English version (Cronbach's alphas between .56 and .89). Test–retest reliabilities were high (rs between .66 and .79). The MAIA also showed good convergent and discriminant validity with other self-report instruments, such as the Five Factor Mindfulness Questionnaire (Baer, Smith, Hopkins, Krietemeyer, & Toney, 2006), the Private Body Consciousness Scale (L. C. Miller et al., 1981), and the trait aspect of the State-Trait Anxiety Inventory (Spielberger, Gorsuch, & Lushene, 1970).

We then investigated changes in the MAIA through CMT. Because this investigation was conducted before the full data of the *ReSource* retest control cohort were available, we recruited an additional sample (n = 80) matched for age, sex, and socio-economic status, who completed the MAIA online twice in the same temporal distance as the training cohorts. We found significant time*training interactions for five of the eight scales. The strongest changes were observed in regulatory aspects of IAw, that is, the extent to which participants use attention to body sensations to regulate distress (d = .72) or to gain insight into their emotional state (d = .40), and the ability to sustain and control attention to body sensations (d = .54). The general appraisal of the body as a safe and trustworthy place increased (d = .30), as well as awareness of the connection between bodily and emotional states (d = .18). No significant changes were observed in the tendencies to worry about or distract from body sensations of pain and discomfort. The mere self-reported noticing of body sensations, which is the aspect predominantly investigated in earlier self-report instruments, was also not significantly altered through the training.

To summarize, we observed significant changes in multiple aspects of IAw through Presence training, with regulatory aspects of IAw being most strongly affected.

Study 3: Psychophysiological coherence and its relationship to interoceptive accuracy

As described in the Introduction, emotional experience is closely linked to physiological arousal. In this study, we investigated whether this link is preserved in memory, that is, do people's recollections of emotional episodes link back to their physiological arousal states during the actual experience? Previous research had shown that people differ in the degree to which their physiological arousal is coherent with their subjective feeling during an actual emotional experience (Golland et al., 2014; Mauss et al., 2005; Sze et al., 2010). In particular, people trained in body observation, such as meditators and dancers, were found to have higher psychophysiological coherence (Sze et al., 2010). Similarly, we assumed that people would differ in the degree to which retrospective accounts of emotional events mirror their physiological arousal during the event. We also sought to clarify the reasons for these individual differences. A straightforward prediction is that people with higher IAcc have better access to their physiological arousal states and will thus encode this information more strongly into their emotional memory, leading to higher psychophysiological coherence. Although theoretically plausible, this has never been empirically demonstrated.

In our study, participants were immersed in virtual reality using a head-mounted display. Participants moved freely through a room for five minutes while we recorded their skin conductance, a measure of sympathetic nervous system activity (Dawson, Schell, & Filion, 2007), and their heart rate, a measure reflecting both sympathetic and parasympathetic arousal (Levy, 1971). Throughout these five minutes, a series of disturbing events occured around them, such as gunshots, the spilling of blood, the appearance of giant spiders, and the floor around them suddenly collapsing, opening the view into the depths below them. After this, participants watched the entire succession of events again on a computer monitor and used a sliding scale to continuously rate the emotional arousal they had felt at any given point of time. We investigated the relationship between physiological arousal during the actual emotional experience and recalled subjective arousal.

We found significant cross-correlations between electrodermal activity and subjectively rated arousal that were of medium to large magnitude (average $r = .43$ and $r = .64$, for the entire period and for the emotionally most intense periods, respectively). Significant medium sized correlations were also observed between cardiac activity and subjectively rated arousal when analyzing the most intense periods of the emotional experience (average $r = .35$). There was considerable interindividual variance in these cross-correlations.

We then investigated the relationship of these psychophysiological coherence measures to IAcc, measured as HBPa (T0 data of Study 1). Individual differences in psychophysiological coherence were correlated to individual differences in IAcc, with small but significant effect sizes ($r = 19$ and $r = .17$ for electrodermal-subjective and cardiac-subjective measures of psychophysiological coherence during the emotionally intense periods, respectively).

To summarize, we found that there is a close correspondence between retrospectively reported arousal and actual physiological arousal during an emotional episode and that the degree of this correspondence is linked to IAcc.

Study 4: Measuring voluntary regulation of heart rate variability and its relationship to altruistically motivated behavior

We were interested in whether CMT would enhance voluntary physiological regulation. We particularly focused on parasympathetic control (estimated by HF-HRV), not only because of its important implications for health and prosocial behavior (see Introduction), but also because improved parasympathetic regulation seemed to be a likely outcome of CMT (see Study 5).

We designed a biofeedback task in which participants saw a ball on a computer screen the altitude of which was determined by Local Power. Local Power is a novel measure of HF-HRV that was developed specifically for this task to allow feedback of HF-HRV with high temporal resolution. LP is highly correlated to established measures of HF-HRV (e.g., peak-to-trough RSA, Grossman, Beek, & Wientjes, 1990: $r = .98$). Biofeedback performance was controlled for respiratory confounds, which is an important concern when interpreting HF-HRV as a measure of parasympathetic (vagal) activity (Grossman, Karemaker, & Wieling, 1991; Quintana & Heathers, 2014). Because increases in HF-HRV had been found to accompany care-giving and altruistic behaviors (Barraza et al., 2015; Gill & Calkins, 2003; J. G. Miller et al., 2015), we hypothesized that regulatory performance in the biofeedback would correlate to individual differences in altruistic behavior (sensu Batson, 2014, p.6). This would not only validate biofeedback performance as a measure of vagal upregulation, but also indicate that the mechanisms of vagal upregulation involved in caring and altruistic behaviors are partially under volitional control. Altruistic behaviors and other types of prosocial behaviors were assessed using factor scores over a large battery of measures, including game-theoretical paradigms, interactive computer tasks, hypothetical distribution tasks, and trait questionnaires (Böckler, Tusche, & Singer, 2016).

We found that participants were able to voluntarily upregulate Local Power. Individual differences in this regulatory ability were correlated to altruistic behavior ($r = .234$, $p < .001$) but not to other, non-altruistic forms of prosocial behavior (such as sacrifices motivated by strategic calculations or adherence to norms) or self-report measures of prosociality.

To summarize, our data show that individual differences in voluntary upregulation of HF-HRV, assessed in a biofeedback setting, correlate to individual differences in altruistic behavior, with theoretical arguments suggesting that both are reflective of individual differences in the capacity to self-induce parasympathetic activity.

Study 5: The relationship of voluntary heart rate variability regulation to the oxytocin receptor gene and its malleability through mental contemplative training

In this study, we continued our investigation of the Local Power biofeedback task as a measure of voluntary parasympathetic (vagal) upregulation (a). We then investigated changes in biofeedback performance through CMT (b).

a) The vagus has been shown to contain high concentrations of oxytocin receptors in humans and other mammals (Boccia et al., 2013; Carter, 2014; Tribollet et al., 1989), and intranasally administered and naturally secreted oxytocin induces increases in HF-HRV in humans (Engert, Koester, Riepenhausen, & Singer, 2016; Kemp et al., 2012; Kubzansky, Mendes, Appleton, Block, & Adler, 2012; Norman et al., 2011). We thus hypothesized that interindividual differences in voluntary parasympathetic upregulation, as measured by our biofeedback task, would be dependent on differences in the oxytocin receptor system. In particular, we expected that carriers of the risk allele (AA) of the oxytocin receptor gene (OXTR) rs53576 polymorphism (Bakermans-Kranenburg & van Ijzendoorn, 2008; McQuaid, McInnis, Matheson, & Anisman, 2015; Riem, Pieper, Out, Bakermans-Kranenburg, & van IJzendoorn, 2011; Tost et al., 2010) would show a lower capacity for parasympathetic regulation. We tested this hypothesis using genomic DNA extracted from blood. The hypothesis was confirmed: AA carriers of rs53576 had significantly lower estimates of voluntary parasympathetic regulation than AG or GG carriers.

b) We then investigated the malleability of voluntary HF-HRV regulation through CMT. Initial training phases, which focus strongly on breath observation (particularly in the Presence module), were hypothesized to foster participant's ability to increase the power of high frequency oscillations (i.e., increase raw Local Power) through breathing modulation. Later training phases, particularly those involving positive social engagement (Porges, 2003a), such as the socio-affective and socio-cognitive training, were hypothesized to increase voluntary parasympathetic control. Training effects in parasympathetic control were hypothesized to be dependent on the oxytocin receptor gene: AA carriers of rs53576, who had previously been shown to be less socially oriented (Bakermans-Kranenburg & van Ijzendoorn, 2008; McQuaid et al., 2015; Riem et al., 2011; Tost et al., 2010), were expected to profit more from the socio-affective and socio-cognitive training modules and thus show greater benefits in terms of voluntary parasympathetic control.

In line with the hypotheses, we found that the initial three months of training (Presence or Affect module) increased participants' ability to upregulate raw Local Power. Trained participants also breathed more slowly than control participants, and these changes in breathing frequency corresponded to the changes in Local Power. After 6 months of training (after Presence plus Affect or Perspective module), there were significant increases in the respiration-controlled parameter of LP upregulation, which is more clearly indicative of increases in parasympathetic control. Increases in this parameter were most pronounced for risk allele (AA) carriers of the oxytocin receptor gene and fully compensated their initial deficits. Model comparisons gave no clear indication that the effects on the two parameters are due to the specific content of the training modules, rather than just training duration.

To summarize, we found further evidence for the Local Power biofeedback task measuring voluntary parasympathetic upregulation, by linking performance in it to the oxytocin receptor system. Furthermore, we found CMT to improve voluntary upregulation of HF-HRV, with mostly breathing-induced changes occurring after 3 months of training and more clearly parasympathetic effects occurring after 6 months of training. The magnitude of training effects was related to the oxytocin receptor gene rs53576 polymorphism.

Discussion

This section discusses the results of the previously described studies. I will first discuss the findings of Studies 1 and 2 together (training-induced changes in interoception). I will then discuss Study 3 (psychophysiological coherence), before turning to the results of Studies 4 and 5 in a joint section (voluntary regulation of heart rate variability—correlates and malleability). These sections discuss the results in the context of the literature, point to interrelations between the grouped studies, mention limitations and future directions as well as specific practical and clinical implications. I will then turn to some further interrelationships between the studies. A final section is dedicated to the larger philosophical and societal implications of the presented research.

Training-induced changes in interoception

In Study 1, we found that CMT enhances IAcc, as measured by a heartbeat perception task. This finding is in line with contemplative literature suggesting increasing levels of bodily awareness with sustained practice (Hart, 1987). It is also coherent with findings in long-term practitioners of CMT demonstrating higher tactile accuracy (Kerr et al., 2008) and slightly higher sensitivity to breathing loads (Daubenmier et al., 2013). Also in line with our findings, both longitudinal and cross-sectional studies on mindfulness meditation have demonstrated training-related structural and functional changes in interoceptive brain networks (Fox et al., 2016; Fox et al., 2014), including the anterior insula, which has been linked to HBPa (Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004). Surprisingly, however, previous studies had not found any effects of CMT on HBPa (Khalsa et al., 2008; Melloni et al., 2013; Nielsen & Kaszniak, 2006; Parkin et al., 2013). I assume that this apparent discrepancy with our findings is due to several reasons: Previous cross-sectional studies employed relatively small samples (between 11 and 30 practitioners) with practitioners from mixed backgrounds and an unclear extent of body focus in their actual practice. Explicit body focus has also been found to reduce with increasing amounts of lifetime contemplative practice in a sample of long-term meditators (Nielsen & Kaszniak, 2006). Thus, HBPa levels may have been indistinguishable from controls because the long-term practitioners had a less bodily oriented practice focus. Of the three published longitudinal studies, two employed extremely brief interventions (1 week with 15 min of daily practice; no compliance control, Parkin et al., 2013, studies 1 and 2). The longest prospective study conducted so far (Parkin et al., 2013, study 3), employed an 8-week MBSR course in 19 participants and found descriptive increases in HBPa of $d = .206$, which did not reach statistical significance due to the small sample and the large standard deviation of HBPa. As we have demonstrated, the effects of training on HBPa build up slowly and cumulatively throughout the training with effect sizes of about $d = .1$ per 3 month module. I therefore assume that previous longitudinal studies have failed to find effects of CMT on HBPa because the interventions were too brief and the samples too small, making statistical analyses underpowered.

Broadening the notion of interoception beyond IAcc, we also investigated multiple dimensions of IAw using the MAIA questionnaire. We found significant training-induced increases in 5 out of 8 MAIA scales. The strongest increases were found for the regulatory aspects of interoception, such as the use of attention to body sensations to regulate distress or to gain insight into the emotional state. Interestingly, changes in the Noticing aspect, that is, the self-ascribed tendency to become aware of bodily signals, were not significant. The self-report data from Study 2 are thus coherent with the objective data from Study 1, which also demonstrate only small and not yet significant effects of the training on objective noticing of bodily signals (HBPa) after the first three months of Presence training. Changes in other dimensions of IAw appear much stronger to participants, backing up earlier qualitative studies in which participants of mindfulness interventions have stressed many corollary mind–body benefits of the training that go beyond the noticing of body sensations (Landsman-Dijkstra et al., 2004; Morone et al., 2008; Schure et al., 2008). This highlights the importance of assessing IAw multidimensionally, particularly when interested in changes therein through mind–body interventions.

Finally, we found that alexithymia decreased over the course of the training, indicating increases in emotional awareness, and that these effects were related to increments in IAcc. This is in line with the vast literature suggesting that the perception of emotion is related to the perception of bodily signals (Craig, 2009; Damasio, 1994; Niedenthal, 2007). Interestingly, changes in IAcc and changes in alexithymia were only related during the Presence module, not during the Affect module. Although both the Presence and the Affect module increase emotional awareness, it seems that only in the Presence module these changes can be explained by improved access to body signals, whereas the Affect module improves emotional awareness through other mechanisms (i.e., acceptance of emotions).

Practical/clinical implications: Accurate perception of body signals and body related appraisals have important implications for mental health (Farb et al., 2015). For instance, Barrett, Quigley, and Hamilton (2016) have recently argued that a core characteristic of depression is a “locked-in brain”, which leads to a construction of emotional reality that is largely disconnected from interoceptive information (also see Michalak, Burg, & Heidenreich, 2012, Remmers & Michalak, 2016). The present research suggests that CMT could help (re)integrating interoceptive information into the mind–body system and thus foster emotional health and self-regulation. Alexithymia, that is a lack of emotional awareness, is common across psychopathologies (Kojima, 2012) and has recently been conceptualized as a “general deficit of interoception” (Brewer, Cook, & Bird, 2016). We demonstrated that training-induced reductions in alexithymia were particularly strong for people with alexithymia scores on the verge to clinical relevance, highlighting the utility of CMT for preventive mental health care.

<u>Limitations:</u> The assessment of IAcc was restricted to HBPa. Although HBPa is the most widely used parameter of IAcc, our knowledge about its relationship to accurate perception of non-cardiac body signals is still very limited (Harver, Katkin, & Bloch, 1993; Herbert et al., 2012; Whitehead & Drescher, 1980). Thus, we cannot infer from our study whether the training has fostered domain-general IAcc or rather HBPa, specifically. However, because attention to heartbeat sensations is barely explicitly targeted in the *ReSource* training, a specific effect on HBPa seems unlikely. Regarding the changes in the MAIA, we have to bear the self-report nature of the data in mind. Multiple distortions may apply from self-serving biases to demand-characteristics (McDonald, 2008). However, assuming that these limitations apply equally to all scales, the data still give us an informative picture about the relative magnitude of the experienced changes in IAw. Finally, in both studies, the effects are established in comparison to retest control groups that do not undergo any training. The studies thus demonstrate that training is more effective in changing IAcc and IAw than no training, but the relative efficacy to other types of interventions (e.g., physical activity) cannot be established by the current data.

<u>Future directions:</u> The data of Study 2 suggest that the largest training effects occur in regulatory aspects of IAw, such as the inclination to direct attention to the body for the regulation of emotional distress. Further investigation of these barely studied aspects of interoception could be fruitful. For instance, in-depth qualitative interviews on *what it is like* to experience and to regulate emotion in an embodied fashion (Petitmengin, 2006) could help

to better understand individual differences in the mind–body relation. Additionally, objective methods could be developed to assess these aspects of interoception. For example, in an experimental setup that aims at the elicitation of emotions, participants could be directed to pay attention to their bodies. The modification of physiological arousal or emotion-related brain activity through bodily focus could serve as an objective measure of body-related self-regulation. A long-term goal could be the establishment of a test battery to quantify different facets of IAw using objective tests (see Burg & Michalak, 2011; Rohde, Adolph, Dietrich, & Michalak, 2014 for another measure that might be incorporated into such a battery).

Psychophysiological coherence

In Study 3, we demonstrated that when remembering their emotional arousal during a prior threatening experience, participants partially recur to the physiological arousal that they exhibited during the actual experience. The extent to which retrospectively rated arousal and actual physiological arousal correspond (psychophysiological coherence) is dependent on IAcc (measured as HBPa). Although three earlier studies have demonstrated temporally synchronous psychophysiological coherence (Golland et al., 2014; Mauss et al., 2005; Sze et al., 2010), this is the first study to demonstrate that this coherence is preserved in retrospective reports of emotional events. Furthermore, our data explain individual differences in psychophysiological coherence by differences in IAcc. These connections have been implicitly assumed in earlier articles (Fox et al., 2012; Sze et al., 2010), but never been empirically demonstrated.

<u>Practical/clinical implications:</u> The observed fidelity of the retrospective, subjective ratings to objective markers of arousal during the actual experience may strengthen our confidence in people's memory for emotional and physiological events. This could serve as a counterweight to views on interospection (Nisbett & Wilson, 1977) and memory (Miron-Shatz, Stone, & Kahneman, 2009) as inherently fallible or unreliable. Although memory failures (and deliberate distortions) certainly do occur, our research implies that we often have good reasons to trust memory, with implications for research, psychotherapeutic and medical contexts, and jurisdiction. Our research suggests that training IAcc may be a way to enhance

retrospective psychophysiological coherence. Enhancing the accuracy of personal emotional memory may be important in conditions such as depression and PTSD, which are often characterized by imprecise (overgeneralized) memory (Barnhofer, Jong-Meyer, Kleinpaß, & Nikesch, 2002; Williams, 1996; Williams et al., 2007).

Limitations: In our study, replaying the visual scenery of the experience to the participants from their own vantage point may have facilitated accurate affective memory. This may have led to higher psychophysiological coherence than expected in other, more naturalistic forms of cued recall.

Future directions: Future studies could investigate health correlates of psychophysiological coherence and its malleability through training of interoception or emotional awareness.

Voluntary regulation of heart rate variability – correlates and malleability

We designed a biofeedback task to measure voluntary physiological regulation, with a particular interest in quantifying voluntary parasympathetic control. We found that, on average, participants were able to voluntarily upregulate HF-HRV. The respiration-controlled upregulatory capacity, indicative of voluntary parasympathetic control, correlated with altruistically motivated prosocial behavior, but not other forms of prosocial behavior that are motivated by strategic calculations or adherence to norms. These data are in line with previous reports showing that incidental increases in HF-HRV accompany or precede altruistic feelings and behaviors (Barraza et al., 2015; Gill & Calkins, 2003; J. G. Miller et al., 2015; Stellar et al., 2015). Our data furthermore suggest that these physiological adaptations that typically accompany altruistic acts are partially under voluntary control. The findings are in line with the Polyvagal Theory, which has implicated parasympathetic (vagal) activity in positive social engagement (Porges, 2003a, 2003b, 2007). They furthermore specify that not all types of prosocial behavior are related to vagal upregulation, but only those rooted in an altruistic motivation (Batson, 2014), that is, care for the wellbeing of others.

The implication of vagal upregulation in mammalian care-giving behavior is also in line with our findings of Study 5, which demonstrate that parasympathetic regulation in the biofeedback task is dependent on the oxytocin receptor gene rs53576 polymorphism. Oxytocin is strongly involved in mammalian care-giving behavior (Feldman, Weller, Zagoory-Sharon, & Levine, 2007; Lee, Macbeth, Pagani, & Scott Young, 2009; Levine, Zagoory-Sharon, Feldman, & Weller, 2007) and has been found to influence interpersonal trust and affiliation in humans (McCall & Singer, 2012). The findings of Studies 4 and 5 together thus point to interconnected genetic, physiological, and behavioral markers which are indicative of individual differences in an emotional-motivational system for care (Panksepp, 2006, 2011).

Plasticity of biofeedback performance through CMT occurred in two phases: After three months, participants showed an improved ability to stimulate increases in raw Local Power, largely driven by breathing modulation. This effect could be explained by improved familiarity with physiological processes and their regulation, in line with the central role of the body in early phases of contemplative practice (Fronsdal, 2001, pp.51ff; Kerr et al., 2013). After six months of training, including a socio-affective or a socio-cognitive module, participants improved in a regulatory parameter that is indicative of voluntary vagal control. This is in line with the role of the vagus in social behavior (Porges, 2003a). The greatest improvements in this parameter were found in AA carriers of the oxytocin receptor gene rs53576 polymorphism, possibly because their initially lower social sensitivity (Bakermans-Kranenburg & van Ijzendoorn, 2008; McQuaid et al., 2015; Riem et al., 2011; Tost et al., 2010) made them most susceptible to the stimulating effects of the interpersonal training.

Practical/Clinical implications: We have shown the biofeedback task to be a marker of parasympathetic control, making it a useful research tool for domains in which this ability matters, ranging from attention (Mathewson et al., 2010) to socio-affective abilities (Shahrestani, Stewart, Quintana, Hickie, & Guastella, 2014). Improvements in the ability to induce high frequency oscillations in HRV, as evident after three months of CMT, has been shown to have beneficial effects in mental and physical disorders, including asthma (Lehrer et al., 2006; Lehrer et al., 2004), cardiovascular disease (Del Pozo, Gevirtz, Scher, & Guarneri, 2004), PTSD (Zucker, Samuelson, Muench, Greenberg, & Gevirtz, 2009) and depression (Karavidas et al., 2007). Later improvements in parasympathetic control may foster the capacities for positive social engagement and altruistic behavior (Barraza et al., 2015; Porges, 2003a; Shahrestani et al., 2014). The data thus suggest that CMT has beneficial effects on individual and societal health.

Limitations: First, we heuristically separated breathing-related and parasympathetic aspects of HF-HRV regulation. However, the relationships between HRV, breathing, and autonomic activity are complex and not fully understood (Eckberg, 2003; Grossman & Taylor, 2007; Porges, 2007; Vaschillo, Vaschillo, & Lehrer, 2006). Second, we find no clear evidence that the parasympathetic effects after 6 months are a result of the social nature of the previously completed training module. The present data cannot differentiate this hypothesis from the hypothesis that parasympathetic effects simply require longer training durations to emerge than breathing-related effects. Third, the limitations of training effects established in comparison to a retest control group discussed above also apply to Study 5.

Future directions: It would be interesting to further gauge the validity of the biofeedback task as a measure of physiological control, by relating performance in it to fluctuations in HF-HRV occurring in naturalistic setting or laboratory experiments. An exciting field for future explorations are the interactions between hormones and neuropeptides (e.g., oxytocin) with central and peripheral nervous (e.g., parasympathetic) activity in human (pro)social behavior. Do individual differences in biological markers give indication for specific vulnerabilities in socio-emotional processes and susceptibility to particular training methods?

Further interrelations between the studies

There are several obvious interrelationships between the studies of this dissertation. I would like to briefly discuss two of these here. First, it is reasonable to assume to that IAcc, operationalized as HBPa (Study 1), and the multiple dimensions of IAw (Study 2) are somehow related. However, in our data, this relationship does not take the form of a straightforward correlation (Kok et al., in preparation). This is in line with several earlier investigations on the topic (Calì, Ambrosini, Picconi, Mehling, & Committeri, 2015; Garfinkel et al., 2015; Leiter-McBeth, 2016; McFarland, 1975). Apparently, individual differences in the accurate processing of bodily signals do not relate to individual differences in the attention that is habitually paid to body sensations or in their appraisal. This could be likened to the process of vision, where we would not necessarily expect optical acuity to relate to the habits of looking or the appraisal of visual experiences (Mehling, 2016). We also need to consider that this lack of correlation comes from a) HBPa being an insufficient proxy of IAcc, which would rather require to be measured as a latent factor of accurate perception across a variety of body signals, or b) distortions in the measurement of IAw caused by the known limitations of self-report.

Second, one might expect interoceptive abilities to predict regulation in the biofeedback task, following the much cited cybernetic postulate that "Every good regulator of a system must be a model of that system" (Conant & Ross Ashby, 1970) and similar arguments about biofeedback by Brener (1974). However, a relationship between IAcc or IAw with biofeedback performance is absent in our data (Bornemann & Singer, in preparation). Early results regarding the relationship between HBPa and heartbeat control (reviewed in De Pascalis, Palumbo, & Ronchitelli, 1991) yielded conflicting results with an equal number of studies showing significant and non-significant correlations. This line of research was, to my knowledge, not continued after 1991. This is striking, particularly because many theories, including recent predictive coding frameworks (Seth & Friston, 2016), explain the health benefits of superior interoception through its effects on physiological adaptation. Further research in this direction is thus clearly warranted. We should, however, bear in mind that there are different levels of the hypothesis that good IAcc predicts good physiological regulation. For the homeostatic processes (e.g., temperature regulation) with their fine-grained subconsciously operating feedback-loops of sensing and regulation (Hardy, 1961), the hypothesis seems justified. Furthermore, emotion regulation (and the resultant/concomitant physiological regulation) first requires awareness of emotions, which is known to be facilitated by IAcc (Füstös, Gramann, Herbert, & Pollatos, 2013; Herbert et al., 2011), lending some evidence to the hypothesis on this level of analysis as well. However, just as we can navigate the program on our TV without knowing how it works, we may often be able to evoke large-scale physiological changes in an organ (e.g., increase HF-HRV) without having an accurate representation of that organ (have good HBPa). Future research on the links between interoception and physiological regulation should distinguish between these different levels of analysis.

Philosophical and societal implications

The current data demonstrate that CMT influences mind–body interactions in various ways: It increases interoceptive accuracy, leading to improved emotional awareness, it improves subjective appraisal of the body and fosters awareness of the mind–body connection, it enhances attention to body sensations for insight and regulation, and it improves physiological control.

These finding could have important implications for policy makers and society in general by underlining the utility of CMT as a low-cost way of improving mental and physical health. At a more abstract level, the data show various interactions and correspondences between mind and body processes, and specifically that mental training changes physiological regulation. These types of findings should not be surprising, neither in the light of ancient contemplative texts (exemplified in the introductory quote of this dissertation), nor in the light of the monistic positions on the mind–body problem endorsed by most psychologists and neuroscientists. However, in Western societies, this knowledge is largely cultivated in a theoretical fashion. There may be more to gain for science and philosophy as well as society at large if we understand the interplay of mental and bodily processes more deeply and in a more embodied fashion.

Divisions of the realm of experience into mind ("res cogitans") and matter ("res extensa") are deeply engrained in our thinking, our language, and our cultural practices (Descartes, 1641/2009; Putnam, 2000). There are pragmatic reasons for such a division, which I also endorsed in this dissertation. Yet, the deep interconnection of these two pragmatically separated levels of description should not slip our minds, particularly when interpreting our scientific investigations about mind–body phenomena. Descriptions in prominent neuroscience articles such as "the brain had already unconsciously made the decision to move even before the subject became aware of it" (Soon, Brass, Heinze, & Haynes, 2008, p.534) can easily be misleading. We usually do not speak of brains making decisions. When we do, as in the cited article, which was widely received scientifically and in the popular press, this can evoke powerful images of ourselves being “under the control of matter”. As I see it, the incantation of this sort of Laplacian demon only works if we implicitly endorse an inconsistent mix of dualism and monism. Seeing through these hidden inconsistencies is not merely of academic interest. Feeling controlled by external circumstances can diminish our sense of self-efficacy with detrimental effects on well-being (Ryan & Deci, 2000). As demonstrated by Vohs and Schooler (2008), viewing oneself as a product of the biological machinery (by being exposed to a philosophical text on material determinism) also decreases our own feelings of responsibility, facilitating immoral behavior.

In my opinion, contemplative mental practice offers a way to gain clarity about the interplay of the seemingly distinct realms of mind and matter. Similar to Varela, I am convinced that meditation can serve as a “methodological remedy to the hard problem” (Varela, 1996) of consciousness (Chalmers, 1995, 2007; also see Varela, Rosch, & Thompson, 1991). Meditation allows the simultaneous observation of physiological and mental processes in the very entity in which they take place, giving rise to insights and qualified intuitions about the nature of mind–body phenomena. Again, this does not only satisfy academic or mystical curiosity but could also transfer to the societal level. An understanding of the deep interconnection between mind and matter may foster feelings of human and global interconnectedness (Ericson, Kjønstad, & Barstad, 2014). This is in line with findings demonstrating links of trait mindfulness to ecologically responsible behavior (Barbaro & Pickett, 2016), and courses in mindfulness meditation (Condon, Desbordes, Miller, & DeSteno, 2013) and the *ReSource* Presence module (Böckler, Tusche, & Singer, in preparation) increasing altruistic behaviors. However, much more research is needed to understand the links between body awareness, the experience of selfhood, and prosocial behavior, and how these are affected by CMT.

To summarize, I see the works of this dissertation embedded in a larger endeavor to understand the interrelationships of mental and bodily processes. This endeavor not only informs our understanding of reality in a philosophical sense but also has potentially huge consequences for our (embodied) understanding of human health and society, impacting the ways we feel and act, individually and collectively.

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List of abbreviations

ANS	Autonomic nervous system
CMT	Contemplative mental training
DNA	Deoxyribonucleic acid
ECG	Electrocardiogram
HF-HRV	High frequency heart rate variability
HRV	Heart rate variability
HBPa	Heartbeat perception accuracy
IAcc	Interoceptive accuracy
IAw	Interoceptive awareness
MAIA	Multidimensional Assessment of Interoceptive Awareness
PTSD	Posttraumatic stress disorder
TAS	Toronto Alexithymia Scale
TC	Training cohort
RCC	Retest control cohort